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EVOLUTION OF EARLY PALEOZOIC FAUNAS IN RELATION TO THEIR ENVIRONMENT[1]

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INTRODUCTION

The evolution of early Paleozoic faunas could be treated with far greater effectiveness if the studies now in progress on the Cambrian faunas were nearer completion. That of the brachiopods is well advanced[2] but the great collections of the U. S. National Museum, representing the crustacea and other invertebrates, have not been studied as to their mode of occurrence, geographic distribution, and biologic and environmental relations. Only a brief summary of the known evidence afforded by the Cambrian rocks and faunas of North America is considered in this paper.

Animals and plants, as now known, are profoundly influenced by

[1] Read before Section E of the American Association for the Advancement of Science, Baltimore meeting, December, 1908.

[2] *Smithsonian Miscellaneous Collections*, Vol. LIII, No. 4, 1908, pp. 139–65.

their environment, hence we will first broadly outline the conditions under which the known marine organisms of Cambrian time lived.[1]

NORTH AMERICAN CONTINENT AT THE BEGINNING AND AT THE CLOSE OF CAMBRIAN TIME

The information obtained since the publication of my first map on this subject in 1891[2] has been assembled on the two accompanying maps by Mr. Bailey Willis. The first map outlines a central mass of pre-Cambrian land, flanked on either side by large barrier islands that served to protect straits, sounds, or seas from the open ocean. Ocean currents flowed through the sounds with varying force and volume, not only from the cold arctic waters to the north, but from the warm tropical region to the south. The relative position of land and sea is based on the present interpretation of the observed characters and distribution of the pre-Cambrian and Lower Cambrian rocks. The distribution of Lower Cambrian faunas indicates the probable courses of the marine currents. A fundamental assumption is that the great ocean basins and continental masses occupied their present relative positions during at least the Algonkian portion of pre-Cambrian time.

The map of the continent at the close of Cambrian time shows that during this period upon the continental area marked changes in the positions of the land and sea took place. Broad shallow seas followed the transgressing shore-line of Middle Cambrian time, offering most favorable conditions for the long-continued development and distribution of marine life.[3] There were undoubtedly deep and shallow seas and bays, cold and warm waters, strong and weak ocean currents of unlike temperatures, protected bays with sandy and muddy bottoms, shore lines gently sloping to deep water, and many conditions promoting the evolution of the faunas through favorable or unfavorable changes in environment, temperature, and food-supply.

The sediments of Cambrian time are mainly those deposited near the shore-line and in adjacent relatively shallow waters. There is little if anything to indicate deposits of the abyssal sea. If the littoral

[1] *Bull. Geol. Soc. Amer.*, Vol. X, 1899, pp. 199–244.

[2] *Bull. U. S. Geol. Survey*, No. 81, 1891, Pl. III.

[3] See theoretic section at the close of Cambrian time: *Bull. U. S. Geol. Survey*, No. 81, 1891, Pl. II.

fauna of the Cambrian sea had begun to work its way down the continental slopes beyond the continental margin into the depths, we can find no evidence of it, either in the Cambrian rocks, or in the character of the present deep-sea fauna.

The life of Lower Cambrian time included Crustaceans (trilobites, ostracods), Mollusca (gasteropods), Molluscoidea (brachiopods), Vermes (annelids), Echinodermata (cystoids), Coelenterata (sponges, corals, jelly-fishes), and the simplest animals, the Protozoa (rhizopods). Immense quantities of microscopic, unicellular plants were undoubtedly present, and, together with the minute Protozoa, must have formed the primary food-supply.[1]

The rôle assigned by Dr. W. K. Brooks to microscopic forms was an important factor in Cambrian time, for the organisms found in the rocks of that period were mainly carnivorous, and were adapted either to straining minute organisms from the water, or to gathering them up from the bottom.

Uniform marine physical conditions over the submerged portions of the continental platform in Lower Cambrian time are indicated by the uniformity of the fauna on opposite sides of the present continent. Whether this fauna was distributed between the east and the west to the north of the central land-area, or south of it, is not definitely determined, yet the absence of Lower Cambrian rocks and fossils from the collections made in the Arctic region, and the presence of closely allied species in the Lower Cambrian rocks of Alabama and California, point to the southern coast-line as the probable highway for the distribution of the littoral fauna. Nothing that suggests the Lower Cambrian fauna is known from South America; in this case, deep water may have been the barrier.

With the advent of Middle Cambrian time land-areas came into existence on the northeast, forming barriers which so affected marine conditions in relation to life that the Paradoxides fauna developed in the Atlantic basin and the Olenoides fauna in the Appalachian region south of the Champlain Valley. To the south and on all sides of the

[1] W. K. Brooks, *Studies from the Biological Laboratory, Johns Hopkins University*, Vol. V, 1893, pp. 136–38. On p. 137 Dr. Brooks says: "The simplicity and abundance of the microscopic forms and their importance in the economy of nature show that the organic world has gradually shaped itself around and has been controlled by them."

central land-area the advancing seas forced the faunas to shift their habitat and either to adjust themselves to the new conditions or to perish. Local isolation for long periods led to the development of new forms, and these, when the barriers were removed, contested and competed for their position and life with other faunas until, by a process of elimination of those least fit to survive, there was hastened the development of a large and varied fauna. With the close of Middle Cambrian time more stable conditions returned, and the era of rapid evolution was checked until the impulse of new conditions of environment and an accumulated tendency to change resulted in the great evolution of life in the lower Ordovician.

LIFE AT THE BEGINNING OF KNOWN CAMBRIAN TIME

The traces of pre-Cambrian life, though very meager, are sufficient to indicate that the development of life was well advanced long before Cambrian time began. The characteristic fossil of the known pre-Cambrian fauna is *Beltina danai*,[1] a crustacean probably more highly organized than the trilobite. The associated annelid trails indicate that this phase of the fauna was also strongly developed. Stratigraphically, this fragment of what must have been a large fauna occurs over 9,000 feet beneath an unconformity at the base of the upper portion of the Lower Cambrian in northern Montana.[2] This fact indicates that it is practically hopeless to search for the first forms of life—those that could leave a trace of their existence—in strata now referred to the Cambrian or early Paleozoic. With this thought in mind we shall consider what is known of the life of early Lower Cambrian (Georgian) time.

The oldest known Cambrian fossils are found deep down in the Lower Cambrian strata of southwestern Nevada and the adjoining Inyo County area of eastern California. In sections 120 miles apart the Lower Cambrian has a thickness of over 5,000 feet, with a great limestone forming the upper 700 to 2,000 feet. Below this limestone calcareous strata occur, but the predominating rocks are sandstones, and arenaceous, siliceous, and calcareous shales. In the lower 400

[1] *Bull. Geol. Soc. Amer.*, Vol. X, 1899, pp. 238, 239.

[2] C. D. Walcott, *Observations of 1908.*

feet of the Waucoba Springs section and the Barrel Spring section south of Silver Peak in western Nevada[1] the fauna includes:

Annelid trails
Protopharetra, sp. undt.
Archaeocyathus, sp. undt.
Ethmophyllum cf. *whitneyi* Meek[2]
Mickwitzia occidens Walcott[3]
Trematobolus excelsis Walcott[4]
Obolella, sp. undt.
Orthotheca, sp. undt.
Holmia rowei, new species
Holmia weeksi, new species

Although this fauna, according to our present knowledge, is the oldest known Cambrian fauna, it includes representatives of the several classes of invertebrates which I will enumerate.

Actinozoa.—The corals are represented by a very primitive form of *Protopharetra*, a small form of cup-shaped *Archaeocyathus*, and a small *Ethmophyllum* closely allied if not identical with *Ethmophyllum whitneyi* (Meek),[5] which occurs higher in the section. The latter is not a notably simple or primitive form of the Archaeocyathinae; on the contrary, it is nearly as far advanced as any species known in the Cambrian.

Vermes.—The annelid borings and trails that occur in and on the sandstones and shales are much like those of the Middle and Upper Cambrian.

Molluscoidea.—The two species of brachiopods represent widely separated genera. *Mickwitzia occidens* Walcott[6] is one of the primitive forms of the Paterinidae, while *Trematobolus excelsis* Walcott[7] is a typical form of the Siphonotretidae. The interval represented by the relative development of *Mickwitzia* and *Trematobolus* is sufficient to convince us that we must look far back in Cambrian, or it may be pre-Cambrian, time for the progenitors of the inarticulate brachiopods.

[1] Walcott, *Smithsonian Miscellaneous Collections*, Vol. LIII, No. 5, 1908, pp. 185–89.

[2] See *Bull. U. S. Geol. Survey*, No. 30, 1886, pp. 81–84.

[3] *Smithsonian Miscellaneous Collections*, Vol. LIII, No. 3, 1908, p. 143.

[4] *Ibid.*, p. 146.

[5] *E. gracile* is considered to be a synonym of *E. whitneyi* (*Bull. U. S. Geol. Survey*, No. 30, 1886, pp. 81–84).

[6] *Smithsonian Miscellaneous Collections*, Vol. LIII, No. 3, 1908, p. 143.

[7] *Ibid.*, p. 146.

Pteropoda.—The forms representing *Orthotheca* are abundant, large, strong, and evidently as well developed as those of the Middle Cambrian.

Crustaceans.—The trilobites thus far found at this horizon are confined to two species of the genus *Holmia*. One of them, *Holmia weeksi*, new species, has many segments, and is more primitive than such forms as *Olenellus thompsoni* Hall[1] and *Holmia bröggeri* (Walcott)[2] of the upper portions of the Lower Cambrian section. The other species, *Holmia rowei*, new species, is of the same general type as *Holmia bröggeri*. The absence of all other trilobite genera is the most marked feature of this early Cambrian fauna.

In the section 100 miles to the south, at Resting Springs, Inyo County, California, a brachiopod closely related to *Billingsella highlandensis* Walcott[3] occurs 2,800 feet below the upper limestone, in association with the trilobite *Holmia rowei*.

Comparing the species in the early Lower Cambrian fauna with the Olenellus fauna, in strata 5,000 feet higher in the section, we find a marked advance in the variety of the later fauna, but we do not know how much of this may be due to the absence, from our collections, of genera and species that may have existed during the deposition of the earlier sediments. In the earlier fauna of the Waucoba section the class characters of the Arthropoda, Mollusca, Molluscoidea, Vermes, and Coelenterata were developed, and while the study of the genera and species adds a little more to our knowledge of the rate of convergence backward in geologic time of the lines representing the evolution of animal life, it, at the same time, proves that a very long time-interval elapsed between the beginnings of life and the epoch represented by the Olenellus fauna.[4]

DISTRIBUTION OF THE LOWER CAMBRIAN (OLENELLUS) FAUNA OVER THE NORTH AMERICAN CONTINENTAL PLATFORM OF CAMBRIAN TIME

The Olenellus fauna lived on the eastern and western sides of a continent that rudely outlined, in its general configuration, the North

[1] See *Bull. U. S. Geol. Survey*, No. 30, 1886, p. 167.

[2] See *Tenth Annual Report, U. S. Geol. Survey*, 1891, p. 638.

[3] *Proc. U. S. National Museum*, Vol. XXVIII, 1905, p. 237.

[4] *Tenth Annual Report, U. S. Geol. Survey*, 1891, p. 595.

American continent of today. Strictly speaking the fauna did not live upon the outer shore facing the ocean, but on the shores of interior seas, sounds, straits, or lagoons that occupied the intervals between the several land-masses that rose from the partly submerged continental platform east and west of the central continental area. On the eastern side, the first land east of the central portion of the continent extended from Alabama northeast along the line of the present Appalachian range to and including the Green Mountains of Vermont. Whether or not the fauna existed in the Connecticut River region to the east of the Green Mountains is unknown. That it occurred further east is shown by its presence in eastern Massachusetts and northwestern Newfoundland. Its presence in a still more easterly basin is proved by its occurrence on the peninsula of Avalon, to the east of the area of Archean rocks crossing central Newfoundland.

It is not my intention to discuss the evidence upon which the assertion of the presence of these various outlying seas, sounds, etc., is based. The evidence of the existence of such bodies of water has been well presented by Dana.[1] What I wish to call attention to now is that the Olenellus fauna lived upon the eastern and western sides of the main North American continental area of late Algonkian and early Cambrian time. This view is sustained by the following observations: (1) The strata containing the Olenellus fauna are known only in the eastern and western portions of the continent; (2) as far as known the Lower Cambrian strata are absent in the interior of the continent; (3) the Upper Cambrian strata are unconformably superjacent to the Algonkian and Archean rocks over the areas where the Middle and Lower Cambrian formations are absent; (4) the strata of the Middle and Lower Cambrian are comformably beneath the Upper Cambrian on the eastern and western sides of the present continent in all sections where the three divisions are present.[2]

The oldest known portion of the Olenellus fauna is limited to that

[1] "Areas of Continental Progress in North America, and the Influence of the Conditions of These Areas on the Work Carried Forward within Them." *Bull. Geol. Soc. Amer.*, Vol. I, 1889, pp. 36–48. "Archean Axes of Eastern North America," *Am. Jour. Sci.*, 3d ser., Vol. XXXIX, 1890, pp. 378–83.

[2] The matter contained in the two preceding paragraphs appeared under the heading "Habitat of the Olenellus Fauna" in the *Tenth Annual Report, U. S. Geol. Survey*, 1891, pp. 556, 557.

section of the Cordilleran area mentioned on p. 197. This fauna was undoubtedly present on the continental shelves to the north and south, and may have been distributed around the southern extremity of the central land-area to the Hudson and Champlain valley region. Future investigation may thus prove that the *Holmia asaphoides* fauna[1] of eastern New York is the oldest part of the Olenellus fauna upon the eastern side of the continent, and that it may be compared with the *Holmia rowei* fauna of the Cordilleran area. The presence in both localities of genera belonging to the Archaeocyathinae indicates that warm currents were passing through the straits or sounds to the east and west of the central continental areas, and that conditions were favorable for a varied fauna. The arenaceous beds (with ripple-marks and trails) of the western Nevada-California area and the interformational conglomerates of eastern New York prove the presence in both areas of relatively shallow water.

The *Olenellus thompsoni* fauna,[2] of late Lower Cambrian time, is widely distributed about the margins of the continental area. Beginning at the Straits of Belle Isle on the northeast, it has been found in eastern Massachusetts, western Vermont, eastern New York, eastern Pennsylvania, and along the Appalachian area as far south as central Alabama. In the Cordilleran area it is known to extend from Inyo County, California, to the Wasatch Mountains of Utah, and northward to the line of the Canadian Pacific Railway in British Columbia.

With the exception of vertebrates, echinoderms, and cephalopods, the class-characters of the early Lower Cambrian fauna of Nevada were well advanced toward the varied and rich fauna of the lower Ordovician.

CONDITIONS DURING MIDDLE AND UPPER CAMBRIAN TIME

The physical conditions of the late Lower Cambrian time continued into early Middle Cambrian time, followed during Middle Cambrian time by a gradual submergence through erosion and probable warping of the surface of most of the continental area south of the Great Lake region.[3] As the marine waters slowly encroached upon this great area and upon the shores adjoining the Appalachian and Cordilleran

[1] *Tenth Annual Report, U. S. Geol. Survey*, 1891, p. 570.

[2] *Ibid.*, p. 569.

[3] *Am. Jour. Sci.*, Vol. XLIV, 1892, pp. 56, 57.

seas the marine life of the times met with conditions favorable to a large development. This is illustrated by the abundant and varied Paradoxides fauna on the Atlantic side and the equally varied Pacific basin Olenoides[1] fauna found in nearly all localities where the Middle Cambrian sediments were deposited.

EVOLUTION OF FAUNAS

That the environment of the faunas of Middle Cambrian time was more favorable for their rapid evolution than that of Lower and Upper Cambrian time is strikingly shown by the stratigraphic distribution of the brachiopods. In the restricted waters of Lower Cambrian time the known brachiopods (of the entire world) were represented by 20 genera and 75 species. In the expanding seas of Middle Cambrian time 31 genera and 243 species are known to have existed. With the more uniform conditions of Upper Cambrian time, and the dying-out of the impulse to variation created by both favorable and unfavorable environments in Middle Cambrian time, the brachiopods decreased in variety and numbers, and are represented by only 23 genera and 137 species.

About the same relative numerical ratios are exhibited by the trilobites but the exact statistics are not yet available. The favorable environment of the Middle Cambrian fauna is well illustrated by the development of *Ogygopsis*, *Asaphiscus*, and *Bathyuriscus* of Cordilleran Middle Cambrian time,[2] genera which are so far in advance of contemporary trilobitic genera that they have sometimes been referred, upon biological grounds, to the Upper Cambrian.[3]

The closing of Cambrian time was accompanied and followed by changes in the relations of the sea and land upon the continental platform that were favorable, like those of Middle Cambrian time, to the

[1] The Olenoides fauna is found on both the eastern and western sides of the northern Pacific Ocean, and the Paradoxides fauna on both sides of the northern Atlantic Ocean. This fauna includes a group of trilobites that are represented more or less fully in the Middle Cambrian rocks of North America, east of the Atlantic basin Paradoxides faunas, and in eastern Asia. The fauna includes: *Olenoides* Meek, *Dorypyge* Dames, *Neolenus* Matthew, *Dorypygella* Walcott, *Damesella* Walcott, *Blackwelderia* Walcott, *Zacanthoides* Walcott, and *Kootenia* Walcott.

[2] See *Bull. U. S. Geol. Survey*, No. 30, 1886, Pls. XXX, XXXI, and *Canadian Alpine Journal*, Vol. I, No. 2, 1908, Pl. 3.

[3] G. F. Matthew, *Trans. Roy. Soc., Canada*, 2d ser., Vol. V, 1899, p. 64.

evolution of new genera and species, and to the existence of multitudes of individuals of the prolific species.

This is not the place for a detailed discussion of the faunas and sediments of the lower Paleozoic. Only the broadest generalizations can be touched upon. I think, however, that sufficient has been said to fix in your minds the following conclusions: (1) That more or less uniform and favorable, even warm, climatic conditions must be appealed to in explanation of the widespread occurrence of almost identical coral-like organisms in the Lower Cambrian, and of the vast number of individuals of various species of trilobites, etc., which existed in Middle Cambrian time; (2) that the rapid and accentuated development of the Middle Cambrian faunas was due in great measure to enlarged opportunity caused by the extension of the Cambrian seas and the consequent shifting of shore-lines and changes in habitat, etc.; (3) that the diversification of the Middle Cambrian fauna, as a whole, may have been due, in a large degree, to the rapid development of narrowly provincial or isolated faunas that were subsequently merged into the more widely distributed fauna by the breaking-down of the restrictive barriers; and (4) that a free and more or less complete interchange of currents in the Cambrian seas was strongly instrumental in producing those cosmopolitan faunas so characteristic of the early Paleozoic. In other words it is evident that the evolution of the early Paleozoic faunas was profoundly influenced by their environment.